

# Seed size variation: magnitude, distribution, and ecological correlates

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## Summary

We examined seed-mass variation in 39 species (46 populations) of plants in eastern-central Illinois, USA. The coefficient of variation of seed mass commonly exceeded 20%. Significant variation in mean seed mass occurred among conspecific plants in most species sampled (by hierarchical ANOVA), averaging 38% of total variance. For most species, within-plant variation was the larger component of total variance, averaging 62% of total variance. Variation in seed mass among fruits within crops was significant in most species tested.

We conclude that variation in seed mass among and within plants is widespread and common. There was little evidence of trade-offs between number of seeds and mean or variance of seed mass, and little correlational evidence of local competition for maternal resources. No consistent ecological (dispersal mode and growth form) correlates of variance of seed mass were evident.

*Keywords:* Seed size variation.

## Introduction

Seed size (mass) can affect seed dispersal and seed predation, as well as seedling establishment, growth, and survival, and thus it has important ecological consequences (Howe and Richter, 1982; Fenner, 1983; Gross, 1984; Hendrix, 1984; Jordano, 1984; Mittelbach and Gross, 1984; Stanton, 1984a, 1985; Weller, 1985; and others). Mean seed sizes have been studied quite extensively, with emphasis on interspecific differences and environmental correlations (Salisbury, 1942; Baker, 1972) and relative intraspecific constancy (Harper *et al.*, 1970). More recently, patterned phenotypic variation of seed mass with plant size (Hendrix, 1984), with season or fruit order (Cavers and Steel, 1984; Fuller *et al.*, 1984; Hendrix, 1984), and with ovule position and parentage (Stanton, 1984b; Mazer *et al.*, 1986) have been reported. However, we know rather little about the extent of variation in seed size, although several authors recently have called attention to its probable importance (Janzen, 1977a, 1977b, 1978, 1982a, 1982b; Capinera, 1979; Hendrix, 1984; Jordano, 1984; Temme, 1986; Thompson, 1984).

We examined several aspects of variation in seed mass. First, the variance was partitioned, to

Table 1. Summary statistics for seeds of 39 species of plants in eastern-central Illinois. For 5 species, data are presented for more than one population. In the columns for partitioning the variance of seed mass, all among-plant entries are statistically significant ( $p < 0.05$ ) proportions of total variance, except zeroes; all among-fruit entries are significant except for *Vitis vulpina*, which is marginally significant ( $0.05 < p < 0.10$ ); blanks in the among-fruits column represent statistically insignificant proportions of the total variance. Principal dispersal mode and growth form are indicated in parentheses: W = wind, A = ant, B = ballistic, VI = vertebrate interiors, VE = vertebrate exteriors, VH = vertebrate hoarders, N = no special means known, H = herb, S = shrub, T = tree, V = vine.

Species	Seed mass (mg)			n	SE <sub>x</sub>	n	var. log x	CV	n (stems)	Partitioning of variance (%)	Among-plant	
	$\bar{x}$	SE <sub>x</sub>	n								Among-fruits	Remainder ('error')
<i>Acer saccharum</i> Marsh. (W,T)	38.179	0.40	472	0.0686	24.06	10	30	-	70			
<i>Aesculus pavia</i> L. (VH,T)												
Pop. 1 (b,d)	4062.000	180.200	101	0.2690	44.59	8	51	39	10			
Pop. 2 (a,c)	4702.000	96.800	181	0.1153	27.71	10	39	11	50			
Total	4473.000	91.300	282	0.1799	34.27	18						
<i>Aesculus glabra</i> Willd. (VH,T)	5401.000	109.800	252	0.2194	32.25	13	56	24	20			
<i>Asarum canadense</i> L. (A,H)	4.581	0.017	1559	0.0236	14.33	10	15	67	18			
<i>Asclepias syriaca</i> L. (W,H)	5.649	0.057	500	0.0737	22.65	20	61	-	39			
<i>Asclepias verticillata</i> L. (W,H)	1.529	0.023	701	0.3163	40.17	10	25	18	57			
<i>Asimina triloba</i> (L.) Dunal. (VI,T)	883.900	4.700	1599	0.0824	22.55	27	47	22	31			
<i>Cassia fasciculata</i> Michx. (B,H)	13.440	0.077	705	0.0254	15.29	10	28	50	22			
<i>Celtis occidentalis</i> L. (VI,T)	114.960	1.507	529	0.0751	30.15	11	62	-	38			
<i>Cercis canadensis</i> L. (W,T)	24.940	0.196	380	0.0259	15.29	4	49	37	14			
<i>Claytonia virginica</i> L. (B & A,H)												
Pop. 1 (a,c)	0.780	0.018	462	0.2889	48.57	24	15	-	85			
Pop. 2 (b,c)	0.816	0.028	190	0.2343	47.22	16	39	-	61			
Pop. 3 (b,d)	0.540	0.022	140	0.2122	48.19	14	45	-	55			
Total	0.746	0.013	792	0.2815	50.22	54						
<i>Cornus racemosa</i> Lam. (VI,T)	24.200	0.183	853	0.0459	22.10	17	36	-	64			
<i>Daucus carota</i> (VE,H)												
Pop. 1 (d)	0.813	0.008	1106	0.1075	31.32	10	25	-	75			
Pop. 2 (c)	0.593	0.007	629	0.0782	28.24	10	41	-	59			
Total	0.733	0.006	1735	0.1181	34.14	20						



determine the magnitude and distribution of intraspecific variation in seed size for 39 species (46 populations):

- (1) What is the magnitude of the variation?
- (2) How is the variation distributed among and within the seed crops of conspecific plants?
- (3) For species with multiseeded fruits, what is the distribution of variation among and within fruits from a given fruit crop?

Next, we examined (by correlation) several predictions about proximal causes of seed-size variation, particularly in relation to competition for maternal resources. If local competition among seeds for maternal resources is a proximate cause of variation in seed mass, several patterns of variation in both mean seed mass and its variance might be expected:

- (1) Within a species, mean seed mass should be negatively correlated with total fruit crop size and with number of seeds per fruit (e.g. Smith and Fretwell, 1974), but the variance of seed mass should be positively correlated with crop size and number of seeds/fruit.
- (2) The variance of seed mass should be smaller in those species with fruits having a large photosynthetic capacity (Bazzaz *et al.*, 1979) available to contribute to the resources acquired by the enclosed seeds and thereby reducing within-fruit competition for resources.
- (3) Plants growing in sunny habitats should have less variation in seed mass than conspecific plants growing in the shade.
- (4) Seeds in late-maturing fruits should be at a competitive disadvantage to those in early-maturing fruits within a fruit crop, and seed mass should decrease (and its variance increase) through the season.

Finally, we examined certain ecological factors for possible correlation with seed-size variation. If the variance (as well as the mean) of seed mass is ecologically important, as many authors (see earlier) have suggested, then we should expect the variance of seed mass to differ among species with differing ecologies. We examined seed-mass variances in our sample with respect to two simple ecological traits as a small start in a search for such patterns: (i) growth form, because growth form may be correlated with overall plant size or with ability to store resources and buffer effects of local variation in resources on seed size (see also Hamrick, 1979); and (ii) dispersal mode, because if variation in seed size affects variation in the seed shadow, then abiotic dispersal and autochory might select for greater variation in seed size than in seeds dispersed by fruit-eating animals that behaviorally produce a variable seed shadow. Also, Salisbury (1942) noted that late-successional species tend to have larger seeds than early-successional species, in association with the greater difficulties of establishment in late succession. The same advantages of larger seeds in later seral stages should hold among populations within a species, although gene flow and/or developmental constraints may prevent a divergence of seed size among conspecific populations. We examined three species for successional trends in mean seed mass.

## Materials and methods

Mature seeds and fruits for all but one species (*Aesculus pavia*, collected in Missouri; see Bertin, 1982) in this survey were collected in autumn 1979 or spring/summer 1980 in Champaign and Vermilion Counties, in eastern-central Illinois (approximately 40°N, 88°W). Whenever possible, the entire fruit production (or 'crop') of a plant was collected. For those species with very large fruit crops, sampling was distributed as evenly as possible over a whole plant or arbitrarily, when dispersal units were harvested from the ground beneath a parent plant (*Ulmus*, *Acer*, some *Tilia*) and when only one fruit per stem was collected (*Asclepias syriaca*). Most species were collected

within 5 km of Urbana, IL, chiefly in Trelease Woods and the adjacent Phillips Tract (an oldfield) 5 km north-east of Urbana. Other species were collected as follows. *Cercis*, *Claytonia*, *Sanguinaria* and *Fraxinus americana* (full names and authorities are given in Table 1) were harvested in and about Kickapoo State Park, 13 km west of Danville, IL. *Hepatica* was collected at the Vermilion River Observatory, about 12 km south-east of Danville. *Staphylea* crops were sampled at Forest Glen County Preserve, 8 km south-east of Westville, IL. *Fraxinus americana* was collected from the banks of Stony Creek, a tributary of the Salt Fork of the Vermilion River, between Urbana and Danville. *Cornus* fruits were harvested at Homer Lake, about 3 km north-west of Homer, IL, and at Trelease. *Tilia* fruits were collected at Trelease and south of Oakwood, Vermilion County. *Juglans* collections were made in Urbana, at Homer Lake, and near Mahomet, IL. Many species in our sample are not known to be clonal; for other species, collections were made from ramets ('stems' in Table 1) usually well separated in space and subjectively judged to be physiologically independent plants.

The seeds of wind-dispersed species (marked 'W' in Table 1) were allowed to air-dry to a constant mass at room temperature; because these seeds naturally disperse in an air-dried state, air-dry weights were measured. All other seeds, in which dry weights were not predictably related to dispersal, were oven-dried to a constant mass at 60–70°C to assess maternal investment. Associated structures (capsules, bracts, wings, pappi, edible pulp, or husks) were separated from the seeds whenever possible. For *Fraxinus* spp., *Daucus*, *Osmorhiza* and *Hepatica*, the mass of the entire dispersal unit was recorded as seed mass because the dispersal structures were not separable from the seeds. For *Tilia* the hard spherical fruit was weighed (not the seed itself). For *Impatiens*, only seeds of chasmogamous flowers were harvested. All 'seeds' were weighed separately to at least three significant digits over the range of seed mass of each species. When fruits contained more than 25 seeds, an arbitrary subsample of 25 seeds or 10% of the seeds in that fruit (whichever was larger) was taken. Plots of the variance versus seed number were used to further determine the level of subsampling required to stabilize the variance. We subjectively excluded seeds that were likely to be inviable (unusually small seeds that contained abnormal-looking embryos or that appeared hollow).

For contrasts of seed-size variation in different habitats, the following habitat definitions were used:

- (1) 'Shade' refers to populations growing in forest interior, 'sun' refers to populations growing in the open or at the edge of a woodlot.
- (2) Early successional habitats for *Claytonia* and *Aesculus pavia* were fields, later successional habitats were forests; for *Daucus*, successional status refers to oldfields of differing ages. Photosynthetic capacity of the fruit was derived in two ways: (i) from published values (e.g. Bazzaz *et al.*, 1979), supplemented by a few unpublished values (R. Carlson, pers. comm.); and (ii) from estimates of fruit shape (surface/volume ratio), which is correlated with photosynthetic ability of fruit (op. cit.) – round, large fruits have lower surface/volume ratios and lower relative photosynthetic ability than do flat, small fruits. For comparisons using method (ii), only fruits at the extremes of the surface/volume ratio spectrum were used; species with fruits of intermediate shape/sizes were omitted.

The coefficient of variation ( $CV = \text{standard deviation}/\text{mean} \times 100$ ) was used for most ecological comparisons of the magnitude of variation, and most comparisons were made using non-parametric statistics. Some controversy exists concerning the appropriate statistical method for comparing variation (e.g. Lande, 1977; Van Valen, 1978; Sokal and Braumann, 1980). Therefore, non-parametric testing of CVs was adopted as a conservative method of analysis of most of the data. Parametric tests of log-transformed data (Lewontin, 1966) were used only for

within-crop correlations of mean and variance of seed weight with seed number per fruit. The 5% significance level was used in all statistical decisions, except as otherwise noted. We present results of marginal significance ( $0.05 < p < 0.10$ ) where they support well-established trends.

## Results

### *Seed mass: magnitude and partitioning of the variance*

The species surveyed are listed in Table 1, with some summary statistics at the population and species levels. The coefficient of variation of seed mass (mass per seed) exceeded 20% in most species and populations surveyed (Table 1) and was greater than 10% in all cases, although none exceeded 100%. The mean CV for our 39 species was about 28%.

A hierarchical ANOVA (Zar, 1984) on the data for each population was used to assess the percentage of the total variance in seed mass that was contributed by variation among plants within populations. For species with multiseeded fruits, the ANOVA assessed variation among fruits within fruit crops and among seed within fruits.

For 37 of 39 species, among-plant variation in seed mass was statistically significant; its contribution to total variance ranged from 11 to 90% (Table 1); the average among-plant variance for all 46 populations was 38% of the total. Variation among plants was particularly large (>75% of total variance) in *Fraxinus americana* (but  $n = 2$  trees only), *Lindera* and *Smilax hispida*; in addition, among-plant variation comprised >50% of the total in *Aesculus pavia* (one population), *A. glabra*, *Asclepias syriaca*, *Celtis*, *Menispermum*, *Prunus* and *Uvularia*. None of the total variance was due to among-plant variation in *Viola* and *Fraxinus pennsylvanica*, while in *Vitis*, *Asarum* and *Claytonia* populations this component of variance was also very low.

In 29 species and one population of *Aesculus pavia*, within-plant variation was the larger component of total variance. Within-plant variance ranged from 10 to 100% of the total variance; the average was 62% of the total variance. Among-fruit variance was statistically significant by the hierarchical ANOVA for 22 of the 24 testable species; this component in *Vitis* was marginally significant. For *Smilax hispida*, among-fruit variance contributed nothing to total variance, perhaps chiefly because multiseededness was very rare. This component of variance was particularly high (>50% of the total) in *Asarum*, *Cassia*, *Impatiens* and *Smilacina*.

### *Proximate causes*

*Correlates with mean seed mass (within species).* Mean seed mass was not correlated with size of the fruit crop per ramet in most of the 12 species for which whole crops were collected (*Claytonia*, *Dicentra* spp., *Geranium*, *Hepatica*, *Phlox*, *Osmorhiza*, *Polygonatum*, *Sanguinaria*, *Smilacina*, *Uvularia*). The sole exception was for the shaded sample of *Dentaria* in which there was a significant negative correlation between mean seed mass and number of fruits per stem (Kendall's tau = -0.16).

At the level of single fruits (in species with >1 seed/fruit), mean seed mass was not significantly correlated, either positively or negatively, with the number of seeds per fruit for most plants sampled (21 species were tested, all those with at least two plants with variable seed numbers/fruit, Pearson product-moment correlation). The exceptions were *Asarum* (7 of 10 plants showed a significant negative correlation) and *Staphylea* (5 of 6 plants showed a significant positive correlation).

For *Dentaria*, the order of fruit production through the season was recorded for each ramet. For the shaded population there was a significant negative correlation of mean seed mass and the order in which fruits developed (Kendall's tau = 0.18).

*Correlates with variation in seed mass.* Variation in seed mass was not correlated with size of the fruit crop per ramet (Spearman rank correlation) within any of the 12 species for which whole crops were collected, nor with fruit order in *Dentaria*.

For *Smilacina* ( $n = 16$ ) and *Phlox* ( $n = 14$ ) seeds from single-seeded fruits had a significantly higher mean CV of seed mass than did seeds from multiseeded fruits in the same crop; Wilcoxon-matched pairs test, normal approximation,  $z = -2.13$ ,  $z = -3.03$ , respectively). For six other species whose fruits varied in number of seeds per fruit, however, there was no significant within-crop difference in variation in mass of seeds from single-seeded and multiseeded fruits.

Seeds from shade-grown plants were significantly more variable than those from sun-grown plants only in *Polygonatum* (sun 17.9,  $n = 7$  stems; shade 24.9,  $n = 10$ ; Kruskal–Wallis test), in which the average number of seeds/plant was also smaller in the shade (sun 177.5, shade 130.4,  $t$ -test). However, no consistent differences were found for *Dentaria*, *Claytonia* or *Aesculus pavia*.

Variation in seed mass was not correlated with the photosynthetic contribution of the fruit in the six species for which photosynthesis data were available. However, those species with fruits with high surface to volume ratios (and high expected photosynthetic capacity) had significantly lower mean CVs ( $n = 8$ ,  $\bar{x} = 17.64$ ) than those with low surface/volume ratios ( $n = 9$ ,  $\bar{x} = 30.93$ ; Wilcoxon 2-sample test,  $p = 0.01$ ).

#### *Ecological correlates*

Variation in seed mass was not detectably related to growth form or dispersal mode (Kruskal–Wallis test; Table 1).

We examined three species for between-population differences in mean seed mass in relation to seral stage. For *Aesculus pavia*, there was no significant difference between seral stage (field and forest; Wilcoxon test). Mean seed mass of late-successional plants of *Daucus* was significantly greater than for early-successional plants (late,  $\bar{x} = 0.79$  mg; early,  $\bar{x} = 0.55$  mg; both  $n = 10$ ,  $p < 0.01$ , Wilcoxon test). However, mean seed mass of *Claytonia* was greater in an early-successional site than in a later stage (early,  $\bar{x} = 0.71$  mg,  $n = 16$ ; late,  $\bar{x} = 0.47$  mg,  $n = 14$ ;  $p < 0.01$ , Wilcoxon test).

## Discussion

### *Magnitude of variation in seed mass*

Thompson (1984) noted that CVs over 5% are often considered 'large' in biological systems and reported seed-size CVs of 14–250% from the literature. By the 5% criterion, all of our 39 species exhibit 'large' CVs, indicating that within-species variation in seed size is considerable.

The review by Harper *et al.* (1970) is frequently cited as evidence of the general constancy of seed weight within species, but this is an erroneous interpretation of their discussion, which dwells on the relative constancy of *mean* seed weight within species. Harper *et al.* (1970) discuss genetic variation among plants in seed size, the results of natural and artificial selection for seed size, as well as both maternal and paternal effects on seed size see (Vander Kloet and Tosh (1984) and Mazer *et al.* (1986) for recent examples of paternal effects). Moreover, other work by Harper's group on *Linum usitatissimum* L. has demonstrated that density influenced the pattern of variation of seed weights (Obeid *et al.*, 1967). Yet somehow this part of their message became overshadowed by other conclusions.

### *Distribution of variation in seed mass*

Significant among-plant variation in seed mass was found in 37 of 39 species examined. The among-plant component of variance was larger than the within-plant component in at least one population of 10 species; the within-plant component was larger in the remainder. Of the 24 species with variable numbers of seeds per fruit, the among-fruit variance was significant for 22 species. Thus, for most of the species examined, maternal parents were producing highly variable offspring and, in most species, parents differed in the size distribution of offspring. These differences among parents are likely to have both genetic and environmental components. For example, parents may differ in levels of plasticity of resource allocation, genetically-based maternal effects on offspring size, or resource levels due to resource distribution patterns.

### *Proximate causes*

We found little evidence of trade-offs between mean seed mass and seed numbers within fruits or within whole seed crops. The principal exception was the shaded population of *Dentaria*, which exhibited a negative correlation of mean seed mass with number of fruits per stem and with fruit order. The failure to detect evidence of trade-offs in most cases may be partially attributable to the effects of plant size, which may have such strong effects on seed number that trade-offs may be evident only when confounding effects of maternal size variation are removed. The simplicity of the trade-off concept has made it very popular in consideration of the evolution of life histories (e.g. Smith and Fretwell, 1974) and examples have been found in some instances (e.g. among plants of *Silene alba*, D. Hanych, pers. comm.). However, it is apparent now that simplistic trade-offs between size and number are often not found (see also Primack, 1978; Hardin, 1984). This does not mean, necessarily, that trade-offs are not important, but it does mean that the scale or conditions in which they may occur need to be examined more thoroughly.

Variation in seed mass was not consistently related (within species) to fruit-crop size, numbers of seeds/fruit, or shadiness of habitat. Although variation in seed mass among species was not correlated with the actual photosynthetic contribution of the fruits, species with fruits with high expected photosynthetic capacity had reduced variation in seed mass. If fruit shape (surface to volume ratio) generally influences fruit photosynthetic capacity and resources available to developing seeds, then variation in seed mass may also be relatively low in other species with high surface to volume ratios.

Thus, if local competition for maternal resources influences seed size, in most cases the effect seems to be small and/or masked by other factors. There may also be strong developmental constraints on seed size, both among related species (Primack, in press) and among plants. Other proximate causes of within-crop variance in seed size are time of fertilization and/or temporal variation in resources available for seed provisioning or the range of offspring quality among seeds (Cavers and Steel, 1984; Fuller *et al.*, 1983; Hendrix, 1984; Thompson, 1984; Stanton, 1984b; Mazer *et al.*, 1986; Temme, 1986).

### *Ecological correlates*

Growth form, dispersal mode, and successional stage were not generally correlated with variation in seed size. If the variance of seed size (and not just the mean) is ecologically important and subject to natural selection, it is likely that ecological patterns in the magnitude of variation occur, because selection for variation would be stronger in some species than in others. Species may differ in their constraints on degree of variation imposed by selection for different levels of plasticity (Marshall *et al.*, 1985), or in allocational priorities among intercorrelated yield components (e.g. optimal seed size may be highly canalized in some species, while seed number is



constrained in others). Finally, if genetic variation in offspring quality within species contributes to size variation (Temme, 1986), then differences in breeding system may be a source of interspecific differences in the magnitude of seed-size variation. Although we have not identified clear general ecological patterns in the magnitude of variation, further examination of this possibility should be encouraged.

#### *General comment*

Many comparisons of the variation in mean seed weight are made with seed numbers or other features often closely associated with plant size (Harper *et al.*, 1970; Obeid *et al.*, 1967). It might be useful to quantify the comparison of variation in seed size and seed number and determine if there are any cases in which seed-size variation is greater than that of seed number. Moreover, few comparisons have been made of the variance of seed weights and the variances of other morphological features. It might be useful to know if seed size is more or less variable than some morphological features that are not related to plant size, which is notoriously variable. For both comparisons, quantitative assessment of the degree of variation is needed.

The existence of within- and among-plant variation in seed size has been known at least since Salisbury (1942). Our results, and those of others cited, show that seed-size variation is both large and common. Variation in seed size is likely to affect the length and density of the seed and seedling shadows around a parent plant, by changing dispersal distances, by altering the range of usable safe sites, or perhaps by determining the outcome of competition among siblings (B. Wallace, pers. comm.) and with other plants. The ecological consequences of differences in seed-size variance need to be determined experimentally and deserve much further exploration.

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